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Ecosystem Heterogeneity Determines the Ecological Resilience of the Amazon to Climate Change

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ABSTRACT

Amazon Forests, which store ~50% of tropical forest carbon and play a vital role in global water, energy and carbon cycling, are predicted to experience both longer and more intensive dry seasons by the end of the 21st century. However, the climate sensitivity of this region remains uncertain: several studies have predicted large-scale die-back of the Amazon, while several more recent studies predict that the biome will remain largely intact. Combining remote-sensing and ground-based observations with a size-and-age structured terrestrial ecosystem model, we explore the sensitivity and ecological resilience of these forests to changes in climate. We demonstrate that water stress operating at the scale of individual plants, combined with spatial variation in soil texture, explains observed patterns of variation in ecosystem biomass, composition, and dynamics across the region, and strongly influences the ecosystem's resilience to changes in dry season length. Specifically, our analysis suggests that, in contrast to existing predictions of either stability or catastrophic biomass loss, the Amazon forest's response to a drying regional climate is likely to be an immediate, graded, heterogeneous transition from high biomass moist forests to transitional dry forests and woody savannah-like states. Fire, logging and other anthropogenic disturbances may, however, accelerate this transition.

Significance Statement

Understanding how changes in climate will impact terrestrial ecosystems is particularly important in tropical forest regions, which store large amounts of carbon and exert important feedbacks onto regional and global climate. By combining multiple types of observations with a state-of-the-art terrestrial ecosystem model, we demonstrate that the sensitivity of tropical forests to changes in climate is dependent on the length of the dry

season, soil type, but also importantly, the dynamics of individual-level competition within plant canopies. These interactions result in ecosystems that are more sensitive to changes in climate than has been predicted by traditional models, but that transition from one ecosystem type to another in a continuous, non-tipping point, manner.

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Amazonia consists of 815 million hectares of rainforest, transitional forest and savannah, stores approximately half of tropical forest carbon (1), and plays a vital role in global water, energy, and carbon cycling (2). While uncertainties in climate predictions for the region remain large (3), recent analyses imply that significant portions of the basin will experience both longer and more intense dry seasons by the end of the 21st century (3-6). There is particular concern about southern Amazonian forests that already experience longer dry seasons than forests in central and western Amazonia (3), and where a trend of increasing dry season length and intensity has already been observed (7). Despite the importance of this region for the global climate, the climate sensitivity of the Amazon forests remains uncertain: model predictions range from a large-scale die-back of the Amazon (8, 9) to predictions that the biome will remain largely intact, and may even increase in biomass (10-12). While some of these differences can be attributed to differences in the predicted future climate forcing of the region (13, 14), accurate predictions of how changes in climate will impact Amazonian forests also rely on an accurate characterization of how the ecosystem is affected by a given change in climate forcing. In this study, we examine the climate sensitivity of the Amazon ecosystem focusing on the mechanisms underpinning changes in forest dynamics and their implications for the timing and nature of basin-wide shifts in biomass in response to a drying climate.

Variation in forest biomass across the Amazon basin (15-17) has been shown to correlate with dry season length (16-18) (Fig. 1), soil texture (16), shifts in stem turnover rate (19) and forest composition (20). In general, high-biomass moist tropical forests occur where dry season length (DSL, defined here as the number of months where precipitation is < 100 mm (6, 9)), is short, and low-biomass savannah-like ecosystems are primarily found when DSLs are long (Fig. 1a). In addition, a significant relationship is observed between regional-scale spatial heterogeneity in above-ground biomass (AGB > 2 kg C m^{-2}) and DSL, with drier places having greater spatial heterogeneity: this pattern is seen at both the scale of 1^{o} (Fig. 1c, r^2=0.88, p<0.01 for remote-sensing based AGB estimates), but also at smaller spatial scales (see *SI Appendix S1*). In other words, in moist areas, where DSL is short, forests have relatively homogenous levels of AGB while, in drier areas, forests are increasingly heterogeneous. As we show below, this observed heterogeneity in response to increasing DSL has important implications for how the structure, composition, and dynamics of Amazon forests will be impacted by changes in climate.

The Ecosystem Demography model (ED2), a process-based terrestrial biosphere model that represents individual plant-level dynamics including competition for light and water (21, 22), was used to investigate the impact of ecosystem heterogeneity on the Amazon forest's ecological resilience to climate perturbations (*SI Appendix S3*). Here the term ecological resilience is used to describe the ability of a forest to maintain fundamental characteristics, such as carbon pools, composition, and structure, despite changes in climate (23). ED2 simulations for the Amazon region, forced with a regional climate dataset derived from *in situ* measurements and remote-sensing observations, correctly reproduce the observed pattern of AGB variability as a function of DSL and soil texture (*Fig. 1, SI Appendix S4*). This is also true for ED2 model simulations for sites where ground-based soil texture, and forest structure, turnover, and composition measurements are available (*Fig. S1, SI Appendix S4*).

An ensemble of model simulations with varying soil texture was used to investigate the mechanisms that underpin the observed variable response to increasing DSL (*SI Appendix S3*). In the model, individual plant productivity is modified by a measure of plant water stress (γ_{WS}) that integrates soil texture, precipitation, and plant transpiration demand such that, as γ_{WS} increases, the plants close their stomata to reduce water loss. In the ED2 ensemble simulations, plot biomass is highly correlated with the average γ_{WS} for the forested sites (defined here as AGB > 3 kg C m^{-2}) (Fig. 2c, r^2=0.96-0.99, p<0.01, *SI Appendix S5*). Associated with changes in AGB that occur as water stress increases are correlated changes in the productivity and composition of the plant canopy (*SI Appendix S6*).

The important role that water stress operating at the scale of individual plants plays in generating these responses is illustrated by comparing the native ED2 model predictions to output from a horizontally and vertically averaged version of the model (ED2-BL), analogous to a conventional 'big leaf' terrestrial biosphere model that represents the canopy in an aggregated manner (*SI Appendix S3*). In the ED2-BL simulations, there is no significant relationship between the spatial heterogeneity of forested sites and DSL (r^2=0.24 p=0.32, Fig. 1a,c). The absence of individual-level plant dynamics in ED2-BL results in a markedly different response to variations in soil texture and dry season length than the native model formulation: biomass initially declines as a function of increasing water stress, but then a tipping point is reached, beyond which the high biomass forest is no longer stable and is replaced by a low biomass savannah (Fig. 2). The result is a bimodal distribution of AGB across the basin in the ED2-BL simulations, in contrast to the continuous distribution seen in the native model formulation and the observations (Fig. 1b). This response mirrors the response seen in other ‘big-leaf’ type ecosystem models (9). In native ED2 simulations, when water stress is prevented from influencing plant productivity, DSL and soil texture no longer impact AGB (*SI Appendix S5* and *Fig. S5*). Taken together, these simulations indicate that the driving mechanism behind the observed heterogeneous response to changes in DSL is the differential performance of individuals within the canopy to declining water availability, and how this response is modulated by soils with different hydrologic properties. Specifically, the size-and-age structure of the ED2 plant canopy results in individuals’ differential access to both light and soil water, influencing the dynamics of individual plant growth and mortality (*SI Appendix S6*). Due to the non-linear nature of functions governing plant growth, mortality, and recruitment, this heterogeneity results in a more continuous, graded response to changes in water stress than the big leaf (ED2-BL) formulation (Fig. 2). The consequence of this heterogeneity in plant-level responses to changes in soil moisture is that soil texture is likely to become increasingly important for controlling AGB as dry season length increases. Soil fertility gradients also influence Amazonian AGB (16-18); however, as we show in *SI Appendix S2,* it does not account for the observed regional-scale pattern of increasing biomass heterogeneity with increasing DSL.

The ED2 biosphere model was used to investigate the expected patterns and time-scales of Amazonian ecosystem response to a one-to-four month change in DSL over the 21st century (6). Earlier analyses have suggested that, by accurately representing the dynamics of individual trees, models such as ED2 that incorporate plant-level dynamics are likely to provide more realistic estimates of forest successional change (21). Forests with a 4-month dry season (24% of the Amazon basin) are projected to lose ~20% of their biomass with a 2-month increase in DSL (range of 11 - 58% loss of AGB dependent on clay content), while drier forests (6-month DSL) respond more rapidly to changes in climate, losing ~29% (20 – 37% loss dependent on clay content) of their biomass with a one month increase in DSL (Fig. 3a, *SI Appendix S7*). As the forests adjust to the new climate regime, the spatial heterogeneity of the forest structure, composition and biomass across the range of soil textures gradually increases. As seen in Fig. 3b, the model predicts that forests in soils with low clay content will be relatively unaffected; however, in high clay content soils, the increase in levels of water stress caused by the onset of a longer dry season will result in marked changes in forest AGB and composition, beginning approximately three years after the perturbation (Fig. 3c). The timescale of the predicted initial ecosystem response is consistent with the results from two field-based through-fall exclusion experiments, which showed declining biomass 3-4 years after a drought was introduced (24, 25). Underlying these predicted changes in AGB and canopy composition are reductions in plant growth and increases in mortality rates (Figs. S14 and S15). While the majority of the change in AGB occurs in the first hundred years, the composition and structure of the forest continues to reorganize for more than two-hundred years after the perturbation (Fig. 3c). Specifically, the simulations predict a substantial decline in the abundance of late-successional trees in high clay content soils. This prediction arises as a simple consequence of the slower rate of growth of late-successional trees that makes them more vulnerable to water stress-induced increases in mortality rates, and less competitive against mid-successional species that are favored by drought-induced increases in understory light levels. This prediction of increased vulnerability of late-successional trees to increases in water stress is, as-yet, untested; however, more generally, our analysis highlights how shifts in climate forcing are likely to drive significant shifts in tropical forest composition and structure over decadal and centennial timescales.

Recent work has hypothesized that two stable ecosystem states may exist along the boundaries of tropical forests and that a tipping point may occur once a climatological moisture threshold is passed (26, 27). Instead, by combining field observations, remote-sensing estimates, and a terrestrial biosphere model, we find no evidence either that an irreversible rapid transition or dieback of Amazon forests will occur in response to a drying climate (8, 9), or that forests will be unresponsive (11, 12). Rather, our results suggest that, at least in the case of Amazonian forests, the ecosystem will exhibit an immediate but heterogeneous response to changes in its climate forcing and that a continuum of transitional forest ecosystem states exists. These conclusions are consistent with experimental observations across Amazonia of short-term drought impacts (28). Furthermore, we find that future climate-induced shifts between a moist tropical forest and dry forest will be a more graded transition accompanied by increasing spatial heterogeneity in forest above-ground biomass, composition, and dynamics across gradients in soil texture. The ability of Amazonian forests to undergo reorganization of their structure and composition in response to climate-induced changes in levels of plant stress acts as an important buffer against more drastic threshold changes in vegetation state that would otherwise occur; however, it also means that the forests are more sensitive to smaller magnitude changes in their climate forcing than previous studies have suggested.

The analysis conducted here intentionally focused on the direct impacts of changes in climate forcing on vegetation, and did not incorporate the effects of soil nutrients, climate driven changes in fire frequency, the effects of increasing atmospheric carbon-dioxide concentrations, the impacts of land transformation, and biosphere-atmosphere feedbacks. With regard to soil nutrients, at the basin-scale, analyses indicate that forest composition, structure, biomass, and dynamics also vary across a gradient in soil fertility (16, 17) with the younger, more fertile soils of western Amazonian supporting forests with lower above-ground biomass and higher rates of biomass productivity and stem turnover relative to the forests of the central Amazon and Guianan Shield, which are located on older, more nutrient-poor soils. Meanwhile landscape-scale studies in the central (29) and northwestern (30) Amazonia have found that more fertile clay soils have higher above-ground biomass than nutrient-poor sandy soils. Further discussion of the impact of soil nutrients can be found in *SI Appendix S2*).

Plant water availability is affected by both the hydraulic properties of soils and plant hydraulic architecture. Our findings of the importance of individual plant water stress on forest response to changes in climate highlight the need for additional studies into both of these important, but relatively under-studied, properties of tropical forests. With regard to soil hydraulic properties, recent studies suggest that the relationship between a soil's texture and its hydraulic properties may differ significantly between tropical and temperate soils (31, 32). However, the impact of these differences on plant water availability remains uncertain. With regard to plant hydraulic architecture, while some measurements exist on rooting properties and vascular architecture of tropical trees (33-36), the above and below-ground hydraulic attributes of tropical trees remain poorly characterized, especially compared to that of temperate trees.

In some areas, particularly those with long dry seasons, increasing water stress is likely to be accompanied by increases in fire frequency, which may act to generate more rapid transitions from a higher biomass forested state to a more savannah-like biome (26, 27). Since these two mechanisms have distinct impacts on forest composition, structure, and function, both must be considered when predicting future responses to changes in climate. The potential impacts of fire on patterns of ecosystem change are discussed in *SI Appendix S1*. Recent modeling studies indicate that CO_2 fertilization may mitigate the impact of increasing water stress (37); however, experimental studies are needed to better quantify the impact of elevated CO_2 concentrations on the physiological functioning of Amazon trees.

While regional patterns of Amazonian above-ground biomass (AGB) are complex, reflecting the impact of multiple factors, our results suggest that plant-level responses to soil texture heterogeneity and changes in DSL are important in explaining the observed basin-wide pattern of variation in Amazonian AGB, providing a mechanistic explanation for the observed correlations between DSL, above-ground biomass, and changes in stand structure and composition (16, 17) . These conclusions may also apply to African and Asian tropical forests; however, important differences exist in the future climate predictions for these regions (38) and their soil edaphic and nutrient characteristics, and historical fire regimes (39-41).

The response of forests to changes in their climate forcing is an emergent ecosystem-level response that is ultimately driven by individual trees responding to changes in their local environments. Non-linearities in the performance of individual plants, such as their rates of photosynthetic assimilation and mortality, as environmental conditions change imply that terrestrial biosphere models need to represent these differential responses of individuals in order to accurately capture emergent ecosystem properties (42). This analysis demonstrates that the conventional approach of modeling average plants in average environments within climatological grid cells underestimates the direct, near-term response of tropical forests to climatological change, but overestimates the direct impacts of larger-scale changes in forcing. Consequently, accurate predictions for the timing and nature of forest responses to changes in climate require consideration of how climate and soils affect the performance of individuals within plant canopies. As we have shown here, models that incorporate plant-level dynamics are able to more accurately characterize observed extant patterns of variation in the structure, composition and dynamics of Amazonian ecosystems, and that accounting for these patterns has important implications for the sensitivity and ecological resilience of Amazon forests to different levels of climatological perturbation.

METHODS

The Ecosystem Demography Biosphere Model (ED2) is an integrated terrestrial biosphere model that incorporates hydrology, land-surface biophysics, vegetation dynamics and soil carbon biogeochemistry and uses a size- and age-structured system of partial differential equations (PDEs) to approximate the individual level dynamics of plant canopies (21, 22, 43). The horizontally and vertically averaged Ecosystem Demography Model (ED2-BL) represents exactly the same biophysical and biogeochemical processes as ED2, but the size- and age-structured canopy is replaced with a horizontally- and vertically- averaged canopy akin to those used by conventional terrestrial biosphere models (*see SI Appendix S3 for further information on the model formulation*).

ED2 and ED2-BL models were run for the entire Amazon basin forced with a rescaled NCEP reanalysis product (44) and observation-based soil maps (45, 46) at 1° resolution, and increasing atmospheric CO_2 (47) (*SI Appendix S3*). The model results were compared against remote-sensing estimates (1, 48) aggregated to the same resolution as the model simulations. Plot-based observations were made on the scale of 0.4-10 ha (20), and were compared against model simulations forced with site-specific inputs (Table *S4*).

The water stress factor (γ_{WS}) was used in both the ED2 and ED2-BL models to scale photosynthesis in response to water stress. γ_{WS} was calculated for each individual (*i*) as:

$$\gamma_{WS}^{i} = 1 - \frac{K\int_0^{RD}(\theta(z)-\theta_{WP})dzC_{root}^{i}}{K\int_0^{RD}(\theta(z)-\theta_{WP})dzC_{root}^{i}+T_{max}^{i}} \qquad (Eq.1)$$

where γ_{WS} ranges from 0 (unstressed) to 1 (stressed). $T^i_{\max}$ is the maximum transpiration (kg H_2O yr^{-1}) for individual i, C_{root} is the root biomass (kgC) for individual i, $\theta(z)$ is the soil moisture (kg H_2O m^{-3}) at soil depth z, K is the root conductance (m^2 kgC^{-1} yr^{-1}), and θ_{WP} is the soil wilting point (kg H_2O m^{-3}). The available soil water (kgH_2O m^{-2}), $\theta(z)-\theta_{\text{WP}}$, is integrated over the rooting depth (RD) of the individual.

Spatial heterogeneity ($\frac{\sigma}{\mu}$) was calculated over 1-month DSL intervals for model simulations and remote-sensing based estimates. These calculations were done at 1-ha resolution for plot-based observations and model simulations for these locations, 500 m and 1-km resolution for remote-sensing based estimates, and 1° resolution for the regional model simulations and remote-sensing based estimates. Due to the relatively low number of plots, the spatial heterogeneity of the plot-based observations was calculated for three DSL categories: 0-2 months, 2-5 months, and 5-8 months.

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Author Contributions:

N.M.L. was involved in study design, model development, ran model simulations, performed data analysis, and wrote the manuscript; K.Z. was involved with model development, ran model simulations and commented on the manuscript; M.L. was involved with model development and provided comments on the manuscript; A.B. provided remote-sensing data and comments on the manuscript; O.P., S.L.L., T.E., T.R.F., and Y.M. provided unpublished field-based observations and comments on the manuscript; E.A., A.A., R.B., A.L.M.M., P.N.V., A.P., and J.E.S.E. provided unpublished field-based observations; P.R.M. was involved in study design, model development, and data analysis, and provided comments on the manuscript.

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Figure captions:

Fig. 1: Change in above-ground biomass with dry season length for remote-sensing based estimates (black and gray circles), ground-based plot measurements (blue triangles), ED2 model output (green circles), and ED2-BL model output (purple circles). Panel b displays the distribution of AGB in the observations and the two models and panel c displays the change in percent biomass variability, coefficient of variation (CV) defined as 1 sigma/ mean. Results are for undisturbed primary vegetation forests.

Fig. 2: Impact of changes in soil clay fraction (panels a and b) and plant water stress (panels c and d) on above-ground biomass (AGB) in the ED2 (panels a and c) and ED2-BL (panels b and d) model simulations. Four climatological conditions are shown, a 2-month dry season, a 4-month dry season, a 6-month dry season and an 8-month dry season.

Fig. 3: Predicted response of forest above-ground biomass and composition to an increase in dry season length (DSL). Panel a shows the change in above-ground biomass after 100 years as a result of increasing dry season length for forests with historic dry season lengths of 2, 4, and 6 months for the range of soil-textures simulated in the ensemble model simulations (N=30). The magnitude of the change in AGB is influenced by soil clay fraction: the mean (solid line), 1σ deviation (shaded region), and minimum and maximum values (dashed lines) are shown. Panels b and c: barplots illustrating the impact of a 2 month increase in dry season (from 4 to 6 months) on a forest situated on a low clay content soil and a forest situated on a high clay content soil. The color of the bars indicates the contribution of mid- and late-successional trees, illustrating the shift in composition caused by the increase in DSL.